



The role of livestock grazing in long-term vegetation changes in coastal dunes: a case study from the Netherlands

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Abstract

The vegetation of coastal sand dunes is characterized by high species diversity and comprises some of the rarest vegetation types in North-Western Europe. Among them are dune grassland communities whose species richness relies on grazing. Those communities are assessed as a priority habitat type under the Natura 2000 legislation. In autumn 1990, Galloway cows and Nordic Fjord horses were introduced in the coastal dunes of Meijendel near The Hague (52° 7'N; 4° 20'E), The Netherlands, to reduce encroachment of tall grasses and shrubs, to develop bare sand patches, and as such facilitating diverse vegetation structures in the dune grasslands. In the 1950s, decades before the introduction of livestock, 41 permanent plots were installed. On average, they were examined every four years. Our study hypothesised that the livestock grazing in the set densities would halt progressive succession and facilitate regressive succession. Up to 1990, we observed an equilibrium between progressive and regressive succession. After 1990, however, our data showed a pronounced progressive succession contradicting the hypothesized effect of the livestock grazing. We relate the main observed patterns with two factors linked to rabbit populations: (i) the myxomatosis outbreak in 1954 and (ii) the rabbit Viral Haemorrhagic Disease (rVHD-1) outbreak in 1989. In addition to livestock grazing, rabbits block progressive succession by feeding on seedlings of shrub and tree species and digging burrows, creating small-scale mosaics of bare sand and initiate blowout development when collapsing. We state that the substantial decrease in rabbit numbers due to the viral diseases likely caused the observed increase of shrubs and trees in the study area's permanent plots. Climate change might have contributed to the observed increase in autonomous blowout development since 2001, as well as a decrease in atmospheric nitrogen deposition since 1990, after a strong increase the decades before.

Keywords

Coastal dunes, European rabbit, livestock grazing, vegetation development

Introduction

The vegetation of coastal dunes is characterized by high species diversity and comprises some of the rarest vegetation types in North-Western Europe. Among them are species-rich dune grasslands (Kuiters et al. 2009). These grasslands are listed as a priority habitat in the Natura 2000 Habitats Directive (H2130; Council of the European Communities 1992).

Since the beginning of industrialization around 1840, biodiversity in The Netherlands has declined dramatically due to changing land use and agricultural intensification, including increasing atmospheric nitrogen depositions (Westhoff 1952; Schaminée and Weeda 2009). Piersma and Olf (2010) calculated a decline of 87% using a species-abundance indicator. In coastal sand dunes, nitrogen has multiplied since 1900 from 5 kg*ha*yr⁻¹ to a maximum of 35 kg*ha⁻¹*yr⁻¹ around 1990 (Noordijk 2007; Kooijman et al. 1998), which is far above the critical limit of 10 kg*ha⁻¹*yr⁻¹ (Bobbink and Hettelingh 2010). As a result, the vegetation in the coastal dunes changed considerably. Dune grasslands, formerly characterized by scattered patches of bare sand, underwent progressive succession and evolved into areas dominated by tall grasses and sedges (e.g., Kooijman et al. 1998; Remke et al. 2009). As a result, shrubs and tree stands expanded extensively (e.g., Van Dorp et al. 1985). These changes led to a monotonous vegetation structure and a considerable loss of plant species diversity in many dune habitats (Ketner-Oostra and Šýkora 2004; Kooijman et al. 1998; Veer and Kooijman 1997). Large herbivores were thought to counteract the process of stabilisation and monotonisation (Van Dijk 1992; Kooijman and De Haan 1995; Provoost et al. 2011). Because large herbivores strongly prefer graminoid species (Lamoot et al. 2005), extensive grazing by domestic livestock has been introduced in many nature reserves in The Netherlands and elsewhere. An overview of 30 years of livestock grazing in The Netherlands by Kuiters (2005) states that still many questions have to be answered to balance the positive and negative consequences. Long-term research based on permanent plots is scarce, but offers insights into the ecosystem dynamics, including the impact of livestock grazing.

Traditionally, coastal sand dunes were used for hunting, small-scale agriculture, animal husbandry, and firewood collection from shrubs and trees. Since the end of the 19th century, anthropogenic management, like livestock grazing, has declined or been discontinued (Vera et al. 2006). In coastal sand dunes, livestock grazing stopped completely (Van Dijk 1992).

During the last decades, much effort has been put into protecting species diversity in the Netherlands. To counteract the decreasing vegetation diversity, livestock grazing has been reintroduced in many nature reserves along the Dutch coast, imitating traditional land-use practices (Van Dijk 1992). This measure was expected to restore the former high biodiversity with an emphasis on the restoration of species-rich dune grasslands (Hoffmann 2002;

Provoost et al. 2004) and to counteract the expansion of shrubs and trees.

Our study aims to investigate the consequences of introducing livestock (Galloway cows and Nordic Fjord ponies) as a management tool in the Meijendel dunes. We hypothesized that this reintroduced grazing management would reduce progressive succession by increasing the area covered by grasslands on the cost of areas covered by shrubs and trees. We further hypothesized an increase of bare sand patches induced by trampling due to the weight of the animals. Since it is well known that rabbits graze to a large extent in dune grasslands and have a significant impact on them (Drees 1988), we discuss the study results in relation to rabbit density and their effect on vegetation diversity in coastal dune grasslands over time.

Study area

The Natura 2000 protected Meijendel dune area is situated north of Den Haag (52°7'N; 4°20'E, The Netherlands), covering an area of 1,800 ha. In the Meijendel area, livestock grazing stopped around 1900 due to the desiccation of vegetation in dune slacks and large dune valleys caused by groundwater extraction for drinking water for Den Haag. In the 1950s, the vegetation map showed a dominance of a mosaic of grasslands, some shrublands, and a few afforested areas (Boerboom 1960). Soon after, a system of artificial recharge for drinking water production was installed, changing the hydrological situation considerably. Part of the previously wet dune slacks were converted into about 100 hectares of infiltration ponds leading to a rising of the groundwater table and a subsequent partial return of wet dune slacks.

The 1985 map distinguished four parallel landscape ecological zones (Van der Meulen et al. 1985): (i) the fore dunes covered mainly with *Ammophila arenaria*, extensively planted for stabilisation purposes for coastal defence, and pockets of shrubs; (ii) the parabolic dunes with a pronounced relief (2–20 m) and calcareous topsoil. They enclose wet dune slacks surrounded by dry areas. The dry areas show mosaics of pioneer dune grasslands (southern exposures), closed dune grasslands (northern exposures), and extensive stands of shrubs including *Hippophae rhamnoides*; (iii) with 5 m – 35 m, the inner dunes are generally higher. Their topsoil is decalcified and supports dune grasslands with short grasses, bryophytes, lichens, open *Hippophae rhamnoides* shrublands, and forest stands; (iv) the large dune valleys situated in between zones (ii) and (iii) contain lime-poor grasslands and deciduous forests on partly flattened and former arable land.

The vegetation of the Meijendel dunes considerably changed after the 1950s (Boerboom 1960; Van der Meulen et al. 1985). Shrubland and forest stands have expanded at the expense of grasslands, a development that continued after 1985 (Van der Hagen et al. 2020b). Grasslands changed from species-rich into species-poor, monotonous vegetation dominated mainly by *Calama-*

grostis epigejos and other tall grasses and the sedge *Carex arenaria*, following the general trend in Dutch coastal sand dunes (Kooijman et al. 1998). As a conservation measure with a focus on the dune grasslands, grazing by Galloway cows and Nordic Fjord ponies (later changed to Konik ponies) in Meijendel was reintroduced in the autumn of 1990 with a livestock density of 0.06–0.07 Units (LLU) $\text{h}^{-1}\text{year}^{-1}$ to counteract the adverse vegetation development. Next to livestock, wild grazers naturally occur in dune systems, including in the Meijendel dune area, which can substantially impact vegetation patterns and diversity. Among them are rabbits that predominantly graze in dune grasslands (priority habitat H2130). They dig burrows inducing blowout development (Aggenbach et al. 2018) and selectively feed on young sprouts of shrubs and trees (Van der Hagen et al. 2020b). However, rabbit disease outbreaks in 1954 and 1989 immediately killed 90–95% of the population, having imminent consequences for the vegetation of the dune ecosystem.

Methods

Permanent plots

In 1952 and 1953, 68 permanent plots were installed in the northern part of Meijendel (Fig. 1) as part of the Dutch 'Network Ecological Monitoring' (Smits et al. 2002). Their sizes range between 4 m^2 and 225 m^2 , related

to the suggested plot sizes for different vegetation types (Schaminée et al. 1995a). The plots are situated in three parts of Meijendel. The western cluster is in the zone of the parabolic dunes (Helmduinen); the other two are situated in the large dune valleys of Kijfhoek and Bierlap (Van der Meulen et al. 1985). The plots cover all successional stages: dune grasslands (*Phleo-Tortuletum ruraliformis*, *Taraxaco-Galietum veri*, *Festuco-Galietum veri*), dune shrubs (*Hippophao-Ligustretum*), and tall shrubland and forests (*Alno-Padion communities*, *Rhamno-Crataegetum*, *Crataego-Betuletum*). In the parabolic dunes, also plots were laid out comprising two rare vegetation types: (i) communities of the *Anthyllido-Silenetum* (Schaminée et al. 1998) and (ii) communities of the *Caricion davallianae* (Schaminée et al. 1995b). All permanent plots are subject to livestock grazing; thus, we could not apply a comparison with ungrazed plots.

Data preparation

We investigate the vegetation changes in the dry part of the dune ecosystem (see Schaminée et al. 1996; 1998), covering more than 95% of the total area. We excluded the permanent plots in the moist and wet parts as they lie outside the study's scope (Van der Hagen 2022). We evaluate 41 permanent plots (60% of the available plots), which over time sum up to 479 relevés. In 1953, almost all dry dune ecosystem vegetation types were present (Appendix I).

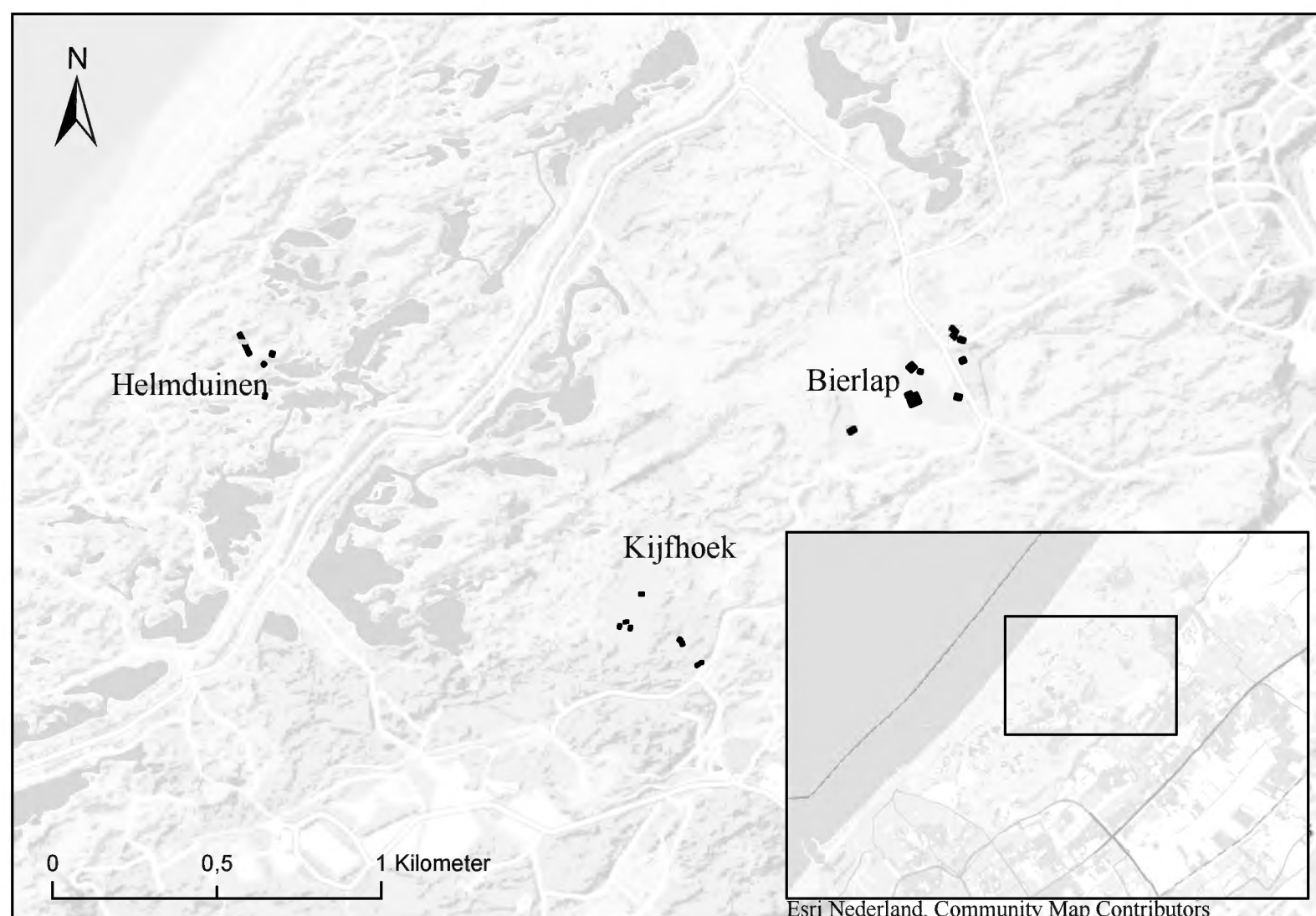


Figure 1. Distribution of the selected permanent plots in Helmduinen, Kijfhoek and Bierlap in Meijendel. Upper left corner: North Sea, right side: inner dune edge near Wassenaar. Blue areas: infiltration ponds for artificial recharge, light blue: dune slacks. Bottom righthand corner: cut-out of Meijendel, surrounded by the cities of The Hague and Wassenaar.

Following the internal homogeneity principle, the plots initially consisted of a homogeneous vegetation patch reflecting a single syntaxon (Braun Blanquet 1951, 1979). Over time, they developed heterogeneously into two or more vegetation types. Initially, the permanent plots were monitored yearly using the Braun-Banquet approach (Braun-Blanquet 1951; Schaminée et al. 1995a). Since the 1970s, the recording cycle decreased to about once in every four years and different scales were applied to record species abundances (e.g., Braun-Blanquet; Barkman, Do-ing & Segal; Londo; see Schaminée et al. 1995a). The varying scales were transformed to an ordinal scale (0-9) using the standard procedure in the database management system of TURBOVEG v2.3 (Hennekens and Schaminée 2001; Hill and Šmilauer 2005).

The syntaxonomic nomenclature follows Schaminée et al. (1996; 1998; 2010), Stortelder et al. (1999), and Kopecký and Hejný (1974). The taxonomy of vascular plants is according to Van der Meijden (2005), mosses according

to Siebel and During (2006), and lichens according to Van Herk and Aptroot (2004).

Analyses

Lammers (2015) applied the TWINSpan algorithm (Hill and Šmilauer 2005) and ASSOCIA (Van Tongeren et al. 2008) in the TURBOVEG v2.3 program to classify the plot-based dataset into clusters. These classification tools were used to identify the various successional stages, ranging from bare sand with open grassland to closed forest. To allocate found vegetation clusters to syntaxonomic names and to define groups of characteristic species, Schaminée et al. (1995a; 1996; 1998) and Stortelder et al. (1999) were applied. Lammers (2015) named the distinguished vegetation clusters according to the defined syntaxonomic species groups (Table 1). To analyse vegetation changes over time, the names of identified plant communities at each point in time were applied. For years

Table 1. Assignment of 32 vegetation clusters into 9 successional stages, successively into 4 succession blocks (4 colours). 1: pioneer grasslands of lime rich soils; 2: dune grasslands of lime rich soils; 3: exclusive dune grasslands of the Zeedorpenlandschap type (Van der Hagen 2022); 4: dune grasslands of acidic topsoils; 5: grassland with tall shrubland elements; 6: semi-closed shrubland with grassland elements; 7: tall shrubland with elements of low shrubland; 8: tall shrubland with forest elements; 9: closed forest stands with tall shrubland elements.

Cluster number	Vegetation cluster	Succession stage
1	<i>Tortulo-Koelerion</i> / <i>Polygalo-Koelerion</i>	1
2	<i>Phleo-Tortuletum ruraliformis</i> / <i>Festuco-Galietum veri</i>	1
3	<i>Phleo-Tortuletum ruraliformis</i> / <i>Violo-Corynephorum</i>	1
4	<i>Cladonio-Koelerietalia</i> / <i>Violo-Corynephorum</i>	1
5	<i>Taraxaco-Galietum veri</i>	2
6	<i>Taraxaco-Galietum veri</i> / <i>Anthyllido-Silenetum</i>	2
7	<i>Taraxaco-Galietum veri</i> with <i>Anthyllido-Silenetum</i> elements	2
8	<i>Anthyllido-Silenetum</i>	3
9	<i>Festuca ovina</i> -[<i>Koelerio-Corynephorum</i>]	4
10	<i>Agrostis capillaris</i> -[<i>Plantagini-Festucion</i>]	4
11	<i>Taraxaco-Galietum veri</i> / <i>Rhamno-Crataegetum</i>	5
12	<i>Festuco-Galietum veri</i> / <i>Rhamno-Crataegetum</i> with <i>Potentilla reptans</i> , <i>Viola canina</i>	5
13	<i>Festuco-Galietum veri</i> / <i>Rhamno-Crataegetum</i> with <i>Agrostis capillaris</i>	5
14	<i>Festuco-Galietum veri</i> / <i>Rhamno-Crataegetum</i> with <i>Asparagus officinalis</i> , <i>Hypericum perforatum</i>	5
15	<i>Festuco-Galietum veri</i> / <i>Taraxaco-Galietum</i> / <i>Rhamno-Crataegetum</i>	5
16	<i>Rhamno-Crataegetum</i> / <i>Festuco-Galietum</i> with <i>Agrostis capillaris</i>	6
17	<i>Rhamno-Crataegetum</i> / <i>Festuco-Galietum</i> with <i>Agrostis stolonifera</i>	6
18	<i>Hippophao-Ligustretum</i> / <i>Festuco-Galietum veri</i>	6
19	<i>Rhamno-Crataegetum</i> / <i>Polygalo-Koelerion</i>	6
20	<i>Hippophao-Ligustretum</i> / <i>Festuco-Galietum veri</i> / <i>Echio-Verbascetum</i>	6
21	<i>Hippophao-Ligustretum</i>	7
22	<i>Rhamno-Crataegetum</i> with <i>Hippophae</i> dominance	7
23	<i>Rhamno-Crataegetum</i> with <i>Sambucus nigra</i>	7
24	<i>Hippophao-Ligustretum</i> / <i>Rhamno-Crataegetum</i>	7
25	<i>Rhamno-Crataegetum</i> with <i>Ligustrum vulgare</i> , <i>Rosa canina</i>	7
26	<i>Rhamno-Crataegetum</i> / <i>Populus tremula</i> -[<i>Alno-Padion</i>] with <i>Agrostis capillaris</i>	8
27	<i>Betula species</i> -[<i>Alno-Padion</i>] = <i>Rhamno-Crataegetum</i> / <i>Betula pubescens</i> -[<i>Alno-Padion</i>]	8
28	<i>Rhamno-Crataegetum</i> / <i>Quercus robur</i> -[<i>Alno-Padion</i>]	8
29	<i>Rhamno-Crataegetum</i> / <i>Populus tremula</i> -[<i>Alno-Padion</i>]	8
30	<i>Rhamno-Crataegetum</i> / <i>Betula pubescens</i> -[<i>Alno-Padion</i>]	8
31	<i>Quercus robur</i> -[<i>Alno-Padion</i>]/ <i>Rhamno-Crataegetum</i>	9
32	<i>Quercus robur</i> - <i>Rhamno-Crataegetum</i>	9

in which a specific plot was not surveyed, the name of the previously identified vegetation cluster continued.

Results

In total 32 vegetation clusters were distinguished, each represented by a varying set of plots. Altogether, the vegetation clusters replicate nine successional stages, each consisting of one to five plant communities (Table 1). The nine successional stages were based on the main syntaxonomical units (Table 2). The nine successional stages were combined into four formation blocks: open dune grasslands (successional stage 1), closed types of grasslands lacking bare sand (successional stages 2, 3, 4 and 5), low and tall semi-open shrubland in mosaic with grassland (successional stages 6 and 7), and tall shrubland and forests (successional stages 8 and 9). We summed shifts of successional stages per year in each permanent plot (Appendix I). Figure 2 gives the share for the years 1953, 1989, 1992, and 2012 of all nine successional stages: the start, years around the livestock introduction and the last year. Table 3 gives the results of the sums of the plots showing the regressive or progressive succession changes in the pre- or post-1990 period to answer our proposed hypothesis on the effect of livestock grazing on regressive succession.

Shifts in successional stages

In 1953, seven out of nine successional stages were present with a dominance of tall shrubland of *Rhamno-Crataege-*

Table 2. Renaming the nine succession stages of Table 1 into a simple syntaxon name with additions.

Succession stage	Vegetation type
1	<i>Phleo-Tortuletum</i>
2	<i>Taraxaco-Galietum veri</i>
3	<i>Anthyllido-Silenetum</i>
4	<i>Festuca-Agrostis</i> basal communities
5	<i>Festuco-Galietum</i> with shrubland elements
6	<i>Rhamno-Crataegetum</i> with grassland elements
7	<i>Rhamno-Crataegetum</i> with elements of low shrubs
8	<i>Rhamno-Crataegetum</i> with forest elements
9	<i>Quercus robur/Rhamno-Crataegetum</i>

Table 3. Relative changes (%) in progressive and regressive succession in the pre-1990 and post-1990 period. The year 1990 is the start of livestock grazing.

Time period	Regressive Succession State	Progressive Succession State
1952-1990	49	51
1991-2012	10	90

tum with forest elements (8), *Taraxaco-Galietum*, a dune grassland of lime-rich soils (2), and the pioneer grassland *Phleo-Tortuletum* (1) (Fig. 2; Appendix I). The rare and species-rich *Anthyllido-Silenetum* (3) was also present in some plots. Two successional stages were absent: the *Festuca-Agrostis* basal community characterized by acidic topsoils (4), and the *Quercus robur* forest stands with tall shrubland elements (9) (Fig. 2).

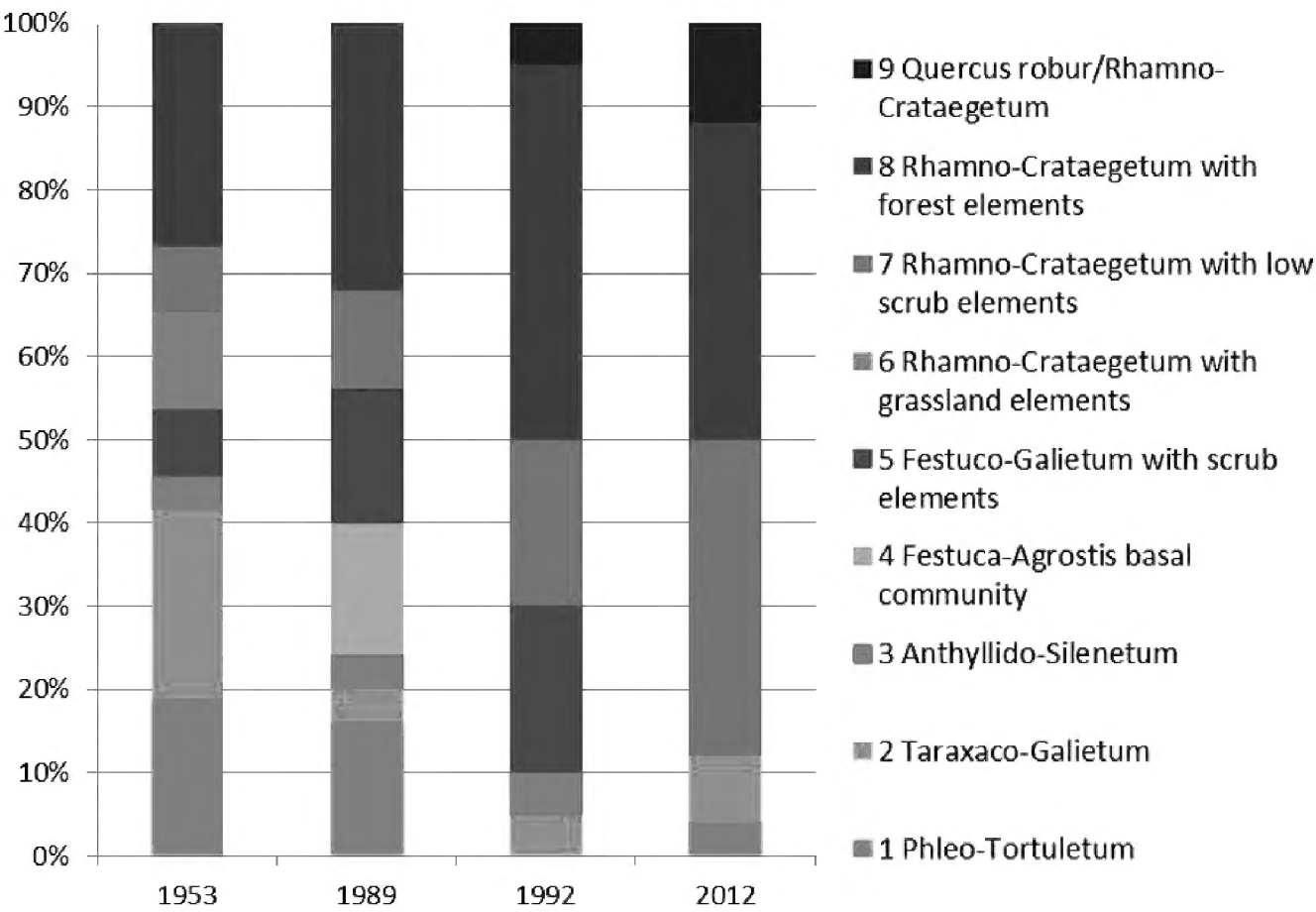


Figure 2. The percentage of permanent plots in the nine successional stages (see Table 1 and Table 2) in four different years: the start of the permanent plot studies (1953), just before introducing livestock (1989), just after introducing livestock (1992) and the last year of the plot study (2012).

In 2012, only five out of nine successional stages were still present in the permanent plots, including early and late successional stages (Fig. 2). In comparison to 1953, dune grasslands *Phleo-Tortuletum* and *Taraxaco-Galietum* (1, 2) had a limited presence in 2012. On the other hand, the *Quercus robur* stands with tall shrubland elements (9) were already present since 2004 (Appendix I) and showed up in an increasing number of plots up to 2012. Over time, the *Rhamno-Crataegetum* with elements of low shrubs (7) and the tall shrubland of *Rhamno-Crataegetum* with forest elements (8) became more prominent with a peak in 1992 (Fig. 2). The successional stages 3, 4, 5, and 6, including the rare *Anthyllido-Silenetum*, disappeared in all plots in 2004 (Appendix I). Overall, changes observed since 1990 predominantly led towards both extremes of successional stages, with a strong emphasis on the late successional stages (Fig. 2; Appendix I).

Progressive versus regressive succession

In the pre-1990 period, when no livestock grazing occurred, we observed a balance in changes between progressive and regressive succession. Since 1990, progressive

succession has dominated after the re-introduction of livestock grazing (Table 3). More precisely, from 1953 until 1970/1972, progressive and regressive changes occurred between all successional stages. After 1970/1972, we observed a slight shift towards progressive succession, with an emphasis on tall shrubland of the *Rhamno-Crataegetum* and, after 1995, also into closed *Quercus robur* forest stands with tall shrubland (9; Appendix I). Both vegetation types became increasingly prominent from 2004 onwards.

The lime-rich dune grasslands of the *Taraxaco-Galietum* (2), substantially present in 1953, decreased after 1972 and again more pronounced after 1981. After 1988, lime-rich grasslands almost completely vanished (Fig. 2; Appendix I). The *Taraxaco-Galietum* returned from 2004 to 2012 in a limited number of plots (Appendix I). Most of the lime-rich dune grasslands (1, 2) shifted towards the *Rhamno-Crataegetum* with grassland elements (6) or with elements of low shrubs (7) (Appendix I). In 1981, grasslands of the *Festuca-Agrostis* basal community (4) with acidic topsoil appeared.

In the post-1990 period with livestock grazing, only a few regressive shifts occurred (10%; Table 3). Post-1990, the *Rhamno-Crataegetum* communities (7, 8) became very prominent. Since 2004, *Quercus robur* forests (9)



Figure 3. The Meijndel dune area: a landscape view with encroachment of high shrubs and the reopening of open sandy dunes after 2001 (A) and a vegetated blowout with an open southern and grassland northern exposed slope with only one rabbit burrow left (B). Photo credit: (A) H.G.J.M. van der Hagen, 2008; (B) F. Witte, 2011.

make up a substantial part of the permanent plots (Appendix I). In 1998, the *Festuca-Agrostis* basal community (4) partly transitioned into lime-rich grasslands (1, 2). Soon after the introduction of livestock in 1990, the sandy pioneer grasslands of the *Phleo-Tortuletum* (1) disappeared but re-occurred after 2004 (Fig. 2; Appendix I). The rare *Anthyllido-Silenetum* (3) persisted from 1953 to 2004, even slightly increasing from 1958 to 1973. In 2004, however, it disappeared in all plots.

Discussion

Despite the expectations derived from theory, livestock grazing in the Meijendel dune area did not halt progressive succession. The reintroduced large livestock should have led to regressive successional processes including the decrease of tall shrublands and forests and a reduced encroachment by tall grasses and shrubs, and an overall increased extent of (species-rich) dune grasslands (Hoffmann 2002; Provoost et al. 2004). We further expected livestock to stimulate the development of bare sand patches by reducing the vegetation cover through trampling. Moreover, despite the re-introduction of livestock grazing, we observed progressive succession and the disappearance of several dry dune grassland successional stages. The only exception we observed was the open and sandy grassland community of the *Phleo-Tortuletum* that reappeared after 2004. In conclusion, we have reasonable doubts that livestock grazing is responsible for the observed changes. Therefore, we rejected our hypothesis and ask ourselves what other driving factors could explain the study's results (Fig. 2; Appendix I).

Grazers: livestock versus rabbits

Three driving factors may explain succession in coastal dune grassland habitats in coastal dunes of North-Western Europe: the almost absence of rabbit grazing and digging, the autonomous return of blowouts after 2001, and the decrease of nitrogen deposition after 1990 (Van der Hagen et al. 2020a; 2020b; Fig. 3). Like livestock, rabbits also feed on grassland vegetation and can significantly reduce above-ground phytomass when occurring in high numbers (Drees 1988). The sharp decline of rabbits due to viral diseases is likely to be the most decisive due to their preference for young nutrient-rich shrub and tree seedlings (Drees and Olff 2001; Van Tongeren 2006; Van der Hagen et al. 2020b). Additionally to the grazing patterns, the burrow digging by rabbits also affects the vegetation composition and structure. The sand taken outside of the burrow creates small patches of bare sand, characteristic for plant communities of the early successional stage of the *Phleo-Tortuletum*. Furthermore, collapsed burrows give way for blowout development (Pluis 1986; Jungerius and Van der Meulen 1988). Both processes create open vegetation structures and facilitate the germination and

growth success of annual and low-competitive plants (Van der Hagen et al. 2020b; Aggenbach et al. 2018).

In 1954 and 1989, the rabbit population in The Netherlands was reduced by 90%-95%, following the disease outbreaks of myxomatosis (Drees and Olff 2001) and the Rabbit Viral Haemorrhagic Disease (RVHD-1; Drees and Van Maanen 2004; Scheffer 2012). After a slight recovery, RVHD-2 reduced the number of rabbits again in 2015 (IJzer et al., 2016). The sharp decline in rabbit numbers due to epidemic viral diseases was a window of opportunity for the establishment and growth of shrub and tree species and the establishment of late successional stages observed in our data.

Up to 1990, we observed an equilibrium of progressive and regressive succession in our study plots (51% progressive shifts versus 49% regressive: Table 3). However, since 1970/1972, a slight shift was detectable (Appendix I) that we link to the fact that it may take some years for a shrub or tree seedling to cover a noticeable area in the plot. Since 1990, when livestock was re-introduced, the observed shifts towards late successional stages were even more pronounced (90% progressive, 10% regressive: Table 3). Shrubs and trees in vegetation types of the *Rhamno-Crataegetum* with grassland (6), shrubs (7) and shrubs with forest elements (8) became more common up to 2012. In 2012, grassland stages of the successional stages of the *Phleo-Tortuletum* and *Taraxaco-Galietum* remained in just a few plots.

Unlike rabbits, livestock are generalist grazers, that do not differentiate between grasses and herbs and do not specifically feed on young seedlings of shrubs and trees (Bokdam 2003; Lamoot et al. 2005; Bakker 2003; Bakker et al. 2009; Smit and Ruifrok 2009; Runhaar et al. 2015). In contrast to the impact of rabbits (Drees 1988; Bakker 2003; McNab n.y.), the livestock grazing pressure of 0.06-0.07 LLU*ha⁻¹*year⁻¹ may have been too low to graze most of the seedlings of shrubs and trees in the Meijendel dune area (Ranwell 1960; Olff and Boersma 1998).

The role of rabbits in dune grasslands conservation

In 1954, the devastating rabbit disease myxomatosis killed most of the rabbits in the Netherlands (Drees and Olff 2001). We did not observe progressive succession before 1970/1972, but we cannot directly attribute the substantial drop in rabbit numbers to our results. However, the effect of reduced grazing and burrow digging by rabbits might be delayed and is likely to be visible after some time. For example, from 1970 to 1972, we observed increasing progressive succession with shifts from the open grasslands (1, 2) and from the *Rhamno-Crataegetum* with grassland elements (6) towards the *Rhamno-Crataegetum* with elements of low shrubs (7) (Fig. 2; Appendix I). Similar results on progressive succession following rabbit reduction were found by Van Groenendael et al. (1982), Bakker (2003) and Van Tongeren (2006).

Growth ring counts on *Crataegus monogyna* revealed a direct link between the high presence of *Crataegus* shrubs and the first three years after the 1954 myxomatosis outbreak (Salman and Van der Meijden 1985), indicating the imminent influence of rabbits on seedling development. In the low presence of rabbits, seedlings can mature even in the presence of livestock or when germinating close to thorny shrubs or poisonous plants like *Jacobaea vulgaris* (Vera et al. 2006). Thorny and long-lasting shrubs, like *Crataegus monogyna*, gradually dominate and nurse seedlings of *Quercus robur* and *Betula* species (Vera et al. 2006). These changes indicate the start of a *Rhamno-Crataegum* with forest elements that gradually changes into forest stands with *Quercus robur*.

In our study, shrublands of *Hippophae rhamnoides* (Table 1: *Hippophae-Ligustretum* plant community in clusters 6 and 7) increased from 1975 to 1990 (Van der Hagen et al. 2020b). After 1990, large parts of the *Hippophae* shrubland collapsed and returned to grasslands. This is due to the lifespan of *Hippophae* of around 40 years, which equals the timespan between the 1954 outbreak of myxomatosis and 1990 (Van der Hagen et al. 2020b) but note that the lifespan of *Hippophae* can vary between 18 and 56 years, incidentally up to 80 years (Zoon 1995; Provoost and Declerck 2020; Decuyper et al. 2020). However, our permanent plot data showed that shrubland shifted mainly into tall shrubs (e.g., *Crataegus monogyna*; Van der Hagen 2020b) from 1972 to 2012 (Fig. 2: 6, 7, 8) and later into *Quercus robur* forest stands (Fig. 2: 9).

In 1989, just before the introduction of livestock, another devastating rabbit disease rVHD-1 killed large parts of the revived rabbit population (Scheffer 2012). As before, we could not see any effect of the substantial reduction of rabbits due to rVHD-1 in our data. However, we observed an apparent increase in late successional stages from 1990 onwards, likely to be explained by the reduced number of rabbits again.

Dry dune grassland processes

At the end of our series of permanent plots in 2012, dry dune grasslands were almost absent except for the *Taraxaco-Galietum* that persisted throughout the study period. The most diverse vegetation type of the 'Zeedorpenland-schap', the *Anthyllido-Silenetum*, vanished from the permanent plots in 2004. This plant community is mostly restricted to the Netherlands and facilitated by multiple aspects of direct and indirect anthropogenic low-impact activities in the dunes, like hunting, small-scale agriculture, and animal husbandry, including livestock grazing (Slings 1994; Van der Hagen 2022). Due to the introduction of livestock, one would expect the return of this grassland stage. Conversely, it disappeared in the Meijndel plots (see also Mourik 2004; Van den Bos 2007; Van der Hagen et al. 2015).

After 2004, we observed a return of the open dune grassland of the *Phleo-Tortuletum* (1). This increase, how-

ever, could not be linked with the 1990 introduced livestock. Several other reasons may be responsible, including the autonomous increase of blowouts since 2001 along the Dutch coast (especially in lime-rich dune habitats like Meijndel), the observed reduction of atmospheric nitrogen deposition (Aggenbach et al. 2018; Van der Hagen et al. 2020b), and climate change with more weather extremes. Heavy rains induce water erosion exposing lime-rich sand vulnerable to wind transport (Jungerius and Van der Meulen 1988).

Critical notes

The permanent plots forming the basis of our study were not randomly distributed when installed in the 1950s. Nevertheless, they covered a meaningful and diverse range of dry grassland communities and as such offered a reliable basis for the observed shifts in Fig. 2. According to Chytrý et al. (2014), utilizing solely permanent plot data for vegetation succession studies can lead to false significant changes and false observation of no changes. Thus, the use of permanent plots might give only limited information on the successional processes occurring in an area over time. However, our study's results align with Van der Hagen et al. (2020b; 2022), proving similar changes in vegetation structure using aerial photographs and with Van der Hagen et al. (2020b) in a since 1975 rabbit enclosure experiment.

Other factors affecting vegetation changes in the dune landscape might interfere with the developments in the permanent plots. For example, nitrogen deposition, peaking around 1990, is likely to have affected progressive succession (Noordijk 2007; Kooijman et al. 2009; Van der Hagen 2020b). Although the lime-rich dune habitat of Meijndel is largely buffered against nitrogen deposition (Aggenbach et al. 2017), nitrogen levels are still high (Bobbink and Hettelingh 2010). Other factors concern climate-change related effects, specifically temperature rise, changes in rainfall and seasonality (KNMI 2013), and the increase of the topsoil temperature, resulting in accelerated soil processes (Bakema et al. 2022).

Conclusion

In contrast to our hypothesis, we found no evidence of regressional succession in relation to livestock grazing. Instead, we observed progressive succession following the introduction of livestock. We consider that the 1954 outbreak of myxomatosis and the 1989 outbreak of RVHD-1 more likely explain our study results, as the effects of rabbits are known to play a crucial role in successional changes of grasslands (Van der Hagen et al. 2020a, 2020b). Unlike cows and horses, rabbits feed selectively on seedlings of shrubs and trees, substantially counteracting progressive succession. Rabbits also create open, sandy patches interspersed in the dune grasslands through dig-

ging. Both factors are likely to combat succession in dry dune grasslands. The observed shifts towards the more open and sandy community of the Phleo-Tortuletum after 2004 is more likely to result from an independent process of recurrent blowouts since 2001 (Aggenbach et al. 2018; Van der Hagen et al. 2020b). Nature conservation measures for the Meijendel landscape conservation area aim to increase the extent of species-rich grasslands listed as an E.U. priority habitat. To reach this goal, we state that year-round livestock grazing with the densities used is largely ineffective (Van der Hagen 2020b; 2022). We further state that rabbit grazing is an excellent tool to combat succession and maintain dry grassland communities. Still, as long as the density of rabbits is low, we recommend that grazing by livestock should be continued, but in other densities and different types of (smaller) livestock. Considering the priority of species-rich dune grasslands in the Natura 2000 legislation and the progressive succession since 1990, felling and pruning trees and shrubs is unavoidable (Van der Hagen 2020b). Probably the best alternative is repopulating the dunes by introducing rVHD-vaccinated rabbits from outside the dunes.

Syntaxa quoted in the text

KOELERIO-CORYNEPHORETEA Klika in Klika et Novák 1941

CLADONIO-KOELERIETALIA Weeda, Doing et Schaminée ined.

Tortulo-Koelerion Tüxen 1937

Polygalo-Koelerion (Boerboom 1960) Weeda, Doing et Schaminée ined.

Plantagini-Festucion Passarge 1964

Alno-Padion Knapp 1942

Caricion davallianae Klika 1934

Phleo-Tortuletum ruraliformis Braun-Blanquet et De Leeuw 1936 nom. inval.

Festuco-Galietum veri Braun-Blanquet et De Leeuw 1936

Violo-Corynephorum Westhoff ex Boerboom 1960

Taraxaco-Galietum veri Boerboom 1957

Anthyllido-Silenetum De Leeuw in Braun-Blanquet et Moor 1938

Hippophao-Ligustretum Melzer 1941

Echio-Verbascetum Sissingh 1950

Rhamno-Crataegetum Sloet van Oldruitenborgh ex Have-man, Schaminée et Weeda ined.

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Appendix I

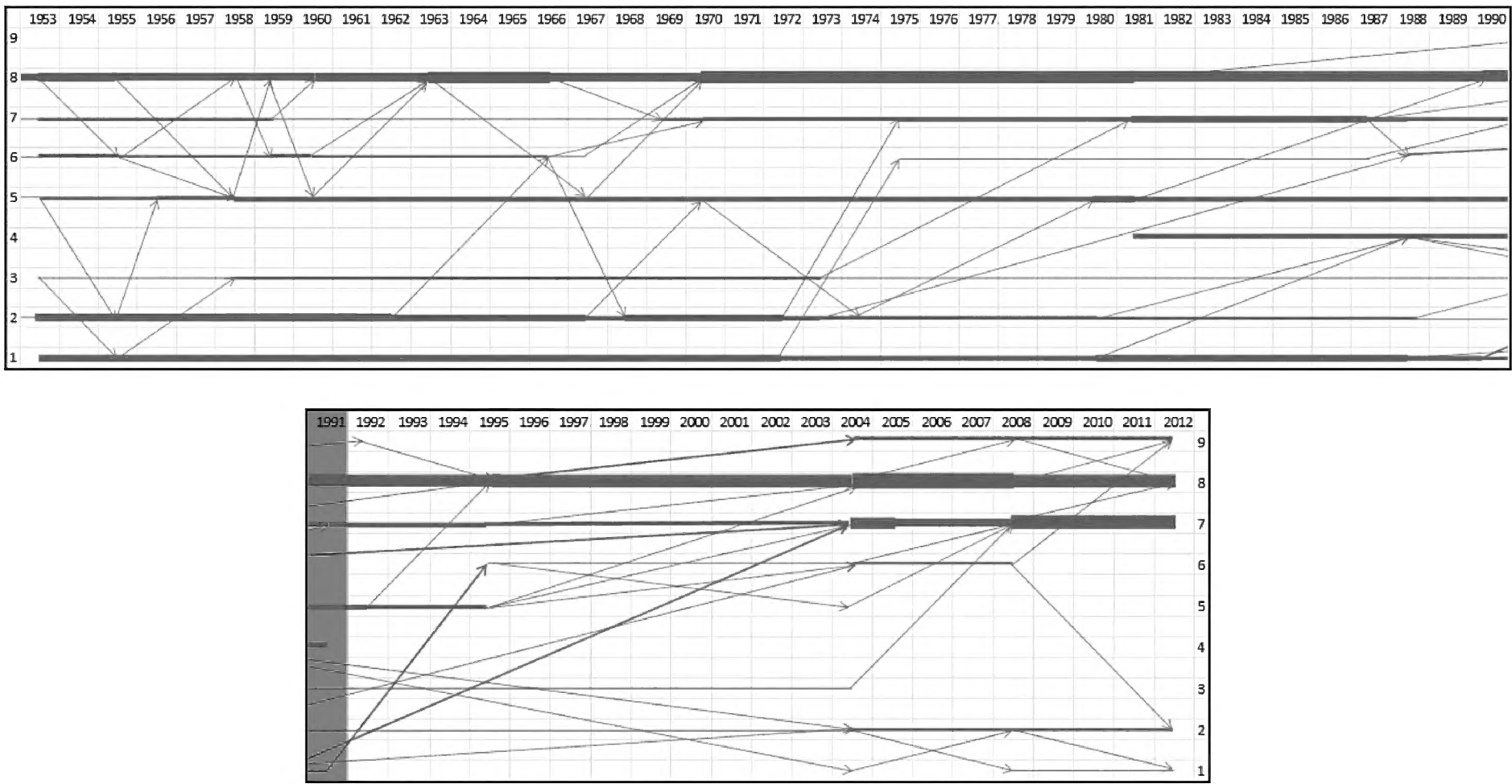


Figure A1. Changes in nine successional stages (Table 1 and Table 2) from 1953 to 2012 based on 32 vegetation clusters of the 41 permanent plots. The thickness of the horizontal lines corresponds with the number of permanent plots in these successional stages; the changes from one to another successional stage are indicated with arrows. The yellow bar represents the start of the livestock grazing. The numbers 1–9 in the left column are explained in Table 2.